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DEMOGRAPHIC MONITORING OF ARABIS FECUNDA POPULATIONS
IN THE SAPPHIRE AND BEAVERHEAD RANGES, MONTANA

1992 Progress Report

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INTRODUCTION

Passage of the Federal Endangered Species Act of 1973 and subsequent recognition of the value of conserving biotic diversity (Wilson 1988) have resulted in many government agencies becoming active in species conservation. Surveys to determine the location and size of populations of rare species are being conducted on public lands throughout the west. These surveys are necessary in any species conservation program; however, knowing the location and size of populations at any one point in time is only the first step in a long-term protection strategy. (Sutter 1986). Extinction is a process requiring an understanding of population dynamics (Menges 1986). Periodic inventories can detect trends but will do little to determine causality or help generate predictive hypotheses (Palmer 1987). Long-term conservation requires a knowledge of many life history parameters including fecundity, recruitment, survivorship, age structure, and population flux. Demographic monitoring techniques can provide information on factors regulating population density and persistence (Palmer 1987). This information, in turn, provides an essential basis for management decisions.

Arabis fecunda Rollins is a rosette-forming perennial in the Mustard Family (Brassicaceae). This recently described species (Rollins 1984) is endemic to highly calcareous, azonal soils in the foothills of the Sapphire Range in Ravalli County and in the Pioneer and Highland ranges of Beaverhead and Silver Bow counties, Montana (Lesica 1985, 1992, Schassberger 1988, Lesica 1992). Arabis fecunda generally occurs on steep, often eroding slopes with low vascular plant density. In Ravalli County, populations of A. fecunda are thought to be threatened by livestock grazing and encroachment by an aggressive exotic weed, spotted knapweed (Centaurea maculosa) (Lesica 1985, Schassberger 1988). In Silver Bow and Beaverhead counties, populations may be threatened by mining activity and livestock grazing. Arabis fecunda is a candidate for listing as a threatened or endangered species by the U.S. Fish and Wildlife Service (USDI-FWS 1990) and is considered threatened in Montana (Lesica and Shelly 1991).

Little is known about the life history and demography of Arabis fecunda populations. The purpose of this study is to determine demographic patterns and variability for this rare species and to use this knowledge to recommend appropriate management strategies for conservation.

METHODS

Study Sites

We conducted our study at Birch Creek and Charleys Gulch in Ravalli County and Lime Gulch and Vipond Park in Beaverhead County, Montana. Both Ravalli County sites are on moderate

southwest-facing slopes; the Birch Creek site is 1430 m above sea level, and the Charleys Gulch site is 1525 m. The two sites are separated by ca. 10 km. At Hamilton, ca. 8 km southwest and 300 m lower, mean temperatures for July and January are 19.4° and -3.8° C respectively, and mean annual precipitation is 32 cm. Zonal vegetation surrounding the sites is foothills Agropyron-Festuca grasslands with scattered Pinus ponderosa Dougl. and Pseudotsuga menziesii (Mirb.) Franco.

The Lime Gulch site occurs on moderate east- and west-facing slopes above a small drainage on the east side of the Pioneer Range at ca 1890 m. The Vipond Park site is on a moderate south-facing slope at 2195 m at the north end of the Pioneer Range. The two sites are separated from each other by ca. 32 km and from the Ravalli County sites by ca. 130 km. For Divide, at 1675 m and north and east of the two sites, mean temperatures for July and January are 17.2° and -7.2° C respectively, and mean annual precipitation is 31 cm. Zonal vegetation around Lime Gulch is Juniperus/Cercocarpus woodland, while it is Artemisia-Festuca-Agropyron steppe at Vipond Park.

Soils at all sites are highly calcareous sandy loams derived from outcrops of metamorphosed calc-silicates or limestone. These soils have a tendency to slump on moderate to steep slopes. Vegetation at these sites is sparse compared to surrounding grasslands and woodlands. Cryptogamic soil crusts are common at Birch Creek, Charleys Gulch and Lime Gulch (Lesica and Shelly 1992a).

Field methods

In 1987 we established two permanent transects, one of 5 and one of 12 contiguous 1-m² plots at both Birch Creek and Charleys Gulch. In 1989 we established two permanent transects of 12 contiguous 1-m² plots each at both Lime Gulch and Vipond Park. We censused Arabis fecunda in 1987-91 at Birch Creek, in 1987-1992 at Charleys Gulch, and 1989-92 at Lime Gulch and Vipond Park. Sampling was conducted in late May at the Ravalli County sites, mid-June at Lime Gulch and late June or early July at Vipond Park. We chose these times because A. fecunda fruits are mature or nearly so, but dispersal has not yet occurred. Plants smaller than 0.5 cm in diameter were not recorded because they could not be reliably distinguished from other species. We did not distinguish between small- and large-size plants in 1987.

Individual A. fecunda plants were mapped and recorded using the following size-life history classification system:

Small (S) = single vegetative rosette < 2 cm in diameter

Juvenile (J) = single vegetative rosette \geq 2 cm in diameter

Multiple-rosette (M) = multiple vegetative rosettes

Reproductive (R) = plants producing 1-many inflorescences

In addition, for each reproductive plant we recorded the number of inflorescences and the number of fruits matured (see Lesica 1987 for further details).

A plant's demographic properties are often more closely correlated with size and life-history stage rather than age (Werner and Caswell 1977, Caswell 1989), although both may be important in predicting an individual's fate (Young 1985). We chose these classes because they are correlated with age as well as size and because they also represent a reasonable compromise between having many categories with too few observations each and few categories with many observations (Vandermeer 1978).

In 1989-92 we collected one fruit from the middle of the inflorescence of each of 25 randomly chosen plants growing near the transects at each site. We counted the number of mature or nearly mature seeds in each fruit to obtain an estimate of seeds/fruit for each site.

We estimated canopy cover of all vascular plants as well as cover of rock, bare soil and basal vegetation in each plot (Daubenmire 1959). We estimated cover to the nearest 5% with two additional classes, 1-3% and 0-1%.

Data analysis

Population growth for year t is the percent change in the size of the sample population between year $t-1$ and year t . It is calculated by $PG = N_t - N_{t-1}/N_{t-1}$. Mortality is defined as the ratio of the number of plants dying between years $t-1$ and t to the number surviving in the same period. Recruitment rate is defined as the ratio of new plants observed in year t to the number of plants surviving from year $t-1$ to year t .

We compared survival rates of uneven-age cohorts present at the start of the study among the sites using the nonparametric logrank test (Pyke and Thompson 1986, Hutchings et al. 1991). Survivorship curves were constructed following methods outlined in Hutchings et al. (1991). Probability values were not adjusted for multiple tests.

For our study, fecundity is defined as the number of fruits per plant. The effects of site and year on fecundity and number of seeds/fruit were analyzed using analysis of variance (ANOVA). We used ANOVA followed by a contrast test to determine the effect of site on bare soil in the plots. Plots within transect cannot be considered independent because they are contiguous. Thus, we used the eight transects as sampling units for the test.

We used correlation and multiple regression analyses to explore relationships between weather variables and Arabis fecunda mortality, recruitment and fecundity. Weather data are

from Hamilton and Divide, the two closest recording stations to the Ravalli County and Beaverhead County sites respectively. Mean monthly deviation from the 30-year normal for temperature and precipitation were calculated for the each year up to and including the spring when demography data were collected (data from National Oceanic and Atmospheric Administration). Take 1991 for example, summer included June, July and August, 1990); fall included September, October and November, 1990; winter included December, 1990 and January and February, 1991; and spring included March, April and May, 1991. Entries for each site and each year were used in the analyses. These samples cannot be considered independent even though responses of *A. fecunda* populations were often very different in the same year (see Results). As a result, significance testing of these regressions is not valid, and reporting probability values is not appropriate. Nonetheless, these analyses provide useful insight into environmental factors affecting demography.

RESULTS

Vegetation

Mean canopy cover estimates for dominant vascular plant species are presented in Table 1. Total basal vegetation cover was generally similar at the four sites (Table 1). Graminoids were common at Lime Gulch, but forbs were more common at the other three sites. Bare soil was more common at Charleys Gulch and Lime Gulch, while rock was more abundant at Birch Creek and Vipond Park. A marginally significant effect on bare soil was attributable to site (ANOVA; $F=4.5$, $P=0.09$), and the amount of bare soil at Birch Creek and Vipond Park compared together was greater than at Charleys Gulch and Lime Gulch ($P=0.03$).

Population Growth

Density of *Arabis fecunda* at the two Pioneer Range transects, Lime Gulch and Vipond Park, was 2-3 times higher than Charleys Gulch or Birch Creek in the Sapphire Range. Over the course of our study the number of *A. fecunda* plants decreased by ca. 10% at Charleys Gulch and by more than 40% at Birch Creek but increased by 37% at Lime Gulch and 65% at Vipond Park (Fig. 1). Population growth varied among years at all sites (Fig. 2). The Charleys Gulch and Lime Gulch populations showed low to moderate among-year variation and displayed similar patterns in growth between 1990 and 1992. On the other hand, the Birch Creek and Vipond Park populations displayed high variability in growth rate and had similar responses in 1990 and 1991. Responses in growth rate between Charleys Gulch-Lime Gulch and Birch Creek-Vipond Park were opposite in sign in three of the five years (Fig. 2).

Figure 1. Density (plants/m²) of Arabis fecunda plants at four study sites in 1987-1992.

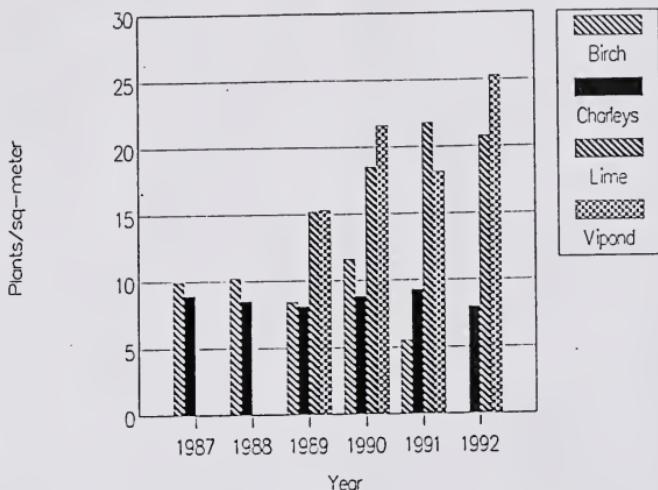


Figure 2. Growth of Arabis fecunda populations at four study sites in 1987-1992 (see Methods for definition of population growth).

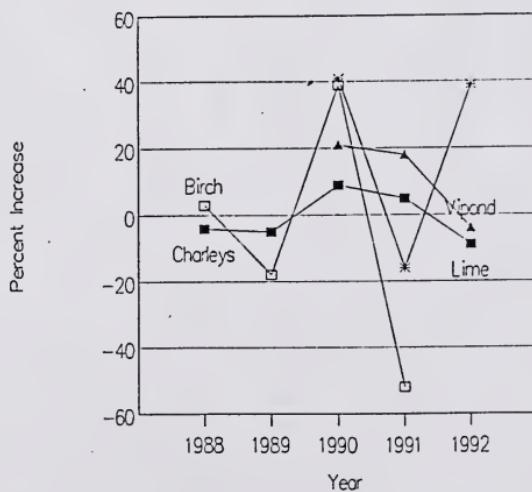


Table 1. Mean ground cover and canopy cover of common vascular plant species in *Arabis fecunda* monitoring transects at four sites.

	Birch Creek East	Birch Creek West	Charleys Gulch East	Charleys Gulch West	Lime Gulch North	Lime Gulch South	Vipond Park East	Vipond Park West
Rock	14	26	5	2	6	6	14	15
Soil	42	52	77	59	52	58	43	40
Basal vegetation	44	23	19	40	43	38	43	48
<i>Agropyron spicatum</i>	2	3	--	--	--	6	6	12
<i>Aristida longiseta</i>	--	--	--	--	--	3	--	--
<i>Carex filifolia</i>	--	--	--	--	--	5	--	2
<i>Carex rossii</i>	--	--	--	--	8	--	--	--
<i>Oryzopsis hymenoides</i>	--	--	--	<1	9	2	--	--
<i>Poa secunda</i>	--	--	3	1	--	--	--	--
<i>Stipa comata</i>	--	--	--	--	7	15	--	--
<i>Alyssum alyssoides</i>	5	--	--	--	--	--	--	--
<i>Artemisia frigida</i>	--	--	2	--	2	2	10	9
<i>Centaura maculosa</i>	24	8	--	30	--	--	--	--
<i>Chrysopsis villosa</i>	--	--	5	<1	--	--	--	--
<i>Haplopappus acaulis</i>	--	--	--	--	--	--	19	13
<i>Lesquerella alpina</i>	3	1	--	--	--	--	--	--
<i>Orytropis besseyi</i>	--	4	--	--	--	--	<1	2
<i>Phlox muscoides</i>	--	--	--	--	--	--	8	11
<i>Physaria geyeri</i>	--	--	2	2	--	--	--	--
<i>Sedum lanceolatum</i>	--	--	--	--	--	3	3	2
<i>Senecio canus</i>	--	--	--	--	3	<1	--	--

Survivorship

Arabis fecunda mortality rates were more variable and generally higher at Birch Creek and Vipond Park (Fig. 3). Temporal patterns of mortality were more similar between Charleys Gulch and Lime Gulch and between Birch Creek and Vipond Park.

Survivorship of the uneven-age 1987 cohort declined significantly more precipitously at Birch Creek than at Charleys Gulch (log-rank test; $LR=19.3$, $P<0.001$), and most of this difference occurred between 1987 and 1988 (Fig. 4a). Decline in survivorship of the uneven-age 1989 cohort was greatest at Vipond Park and least at Charleys Gulch (Fig. 4b). Survivorship curves from Charleys Gulch and Lime Gulch were not significantly different ($LR=1.4$, $P=0.23$), but the Vipond Park survivorship curve was different from both Lime Gulch ($LR=10.2$, $P=0.001$) and Charleys Gulch ($LR=9.5$, $P=0.001$). At Charleys Gulch and Lime Gulch the probability of death was nearly constant, while at Birch Creek and Vipond Park younger plants had a higher chance of dying.

Recruitment

Recruitment of *Arabis fecunda* varied among sites and years but was generally higher and more variable at Birch Creek and Vipond Park (Fig. 5). The best years for recruitment were not the same among the four sites. Recruitment was high at Charleys Gulch and Lime Gulch in 1991 but not at Birch Creek or Vipond Park. 1988 was a strong recruitment year at Birch Creek but not Charleys Gulch, and 1992 was the highest recruitment year at Vipond Park but was lowest for both Charleys Gulch and Lime Gulch. Recruitment was high at all sites in 1990 (Fig. 5.). There was a strong negative correlation between mortality rate and recruitment rate among the four sites over the six years of the study ($N=15$, $r=-.63$, $P=0.01$).

Fecundity

The percent of each *Arabis fecunda* populations that flowered and produced fruit varied among years (Fig. 6). On years of high recruitment a larger percentage of plants are new recruits and less likely to flower. Thus, the percentage of plants flowering is expected to be lower in years of high recruitment; however, this does not appear to be the case (compare Fig. 5 and 6). Percent reproductive plants was at least 15% at all sites in all years except there were few reproductives at Birch Creek and Charleys Gulch in 1988 and at Lime Gulch in 1989 (Fig. 6). Percent reproductives was highest in 1990 at all sites except Birch Creek.

The number of fruits per reproductive *A. fecunda* plant varied greatly among sites and years (Fig. 7). Site was a

Figure 3. Mortality rate of Arabis fecunda populations at four study sites in 1987-1992 (see Methods for definition of mortality rate).

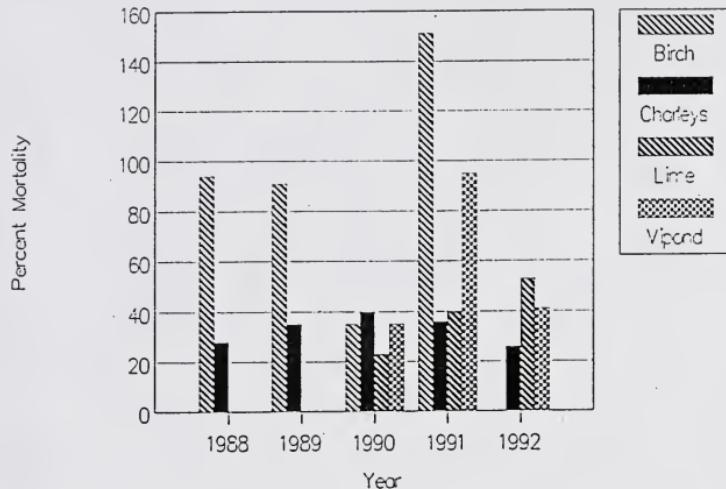


Figure 4. Survivorship of uneven-age cohort (A) at Birch Creek and Charleys Gulch in 1989-91 and (B) at Charleys Gulch, Lime Gulch and Vipond Park in 1989-92.

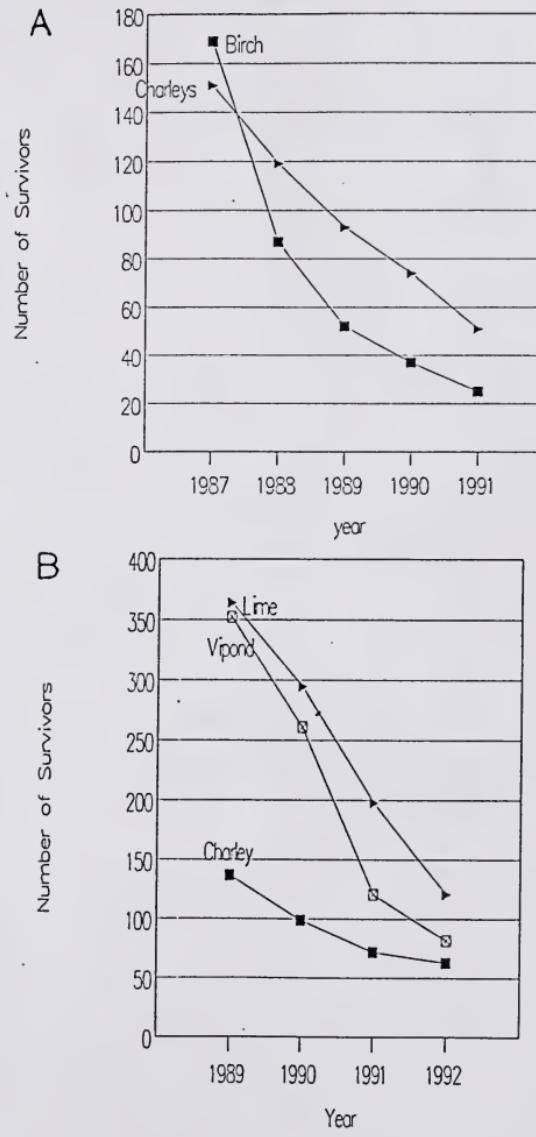


Figure 5. Recruitment rate of *Arabis fecunda* populations at four study sites in 1987-1992 (see Methods for definition of recruitment rate).

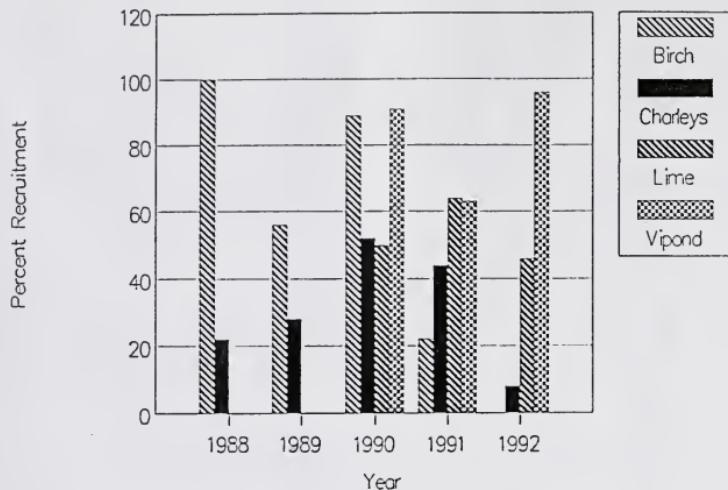


Figure 6. Percent of *Arabis fecunda* plants that produced flowering inflorescences at four study sites in 1987-1992.

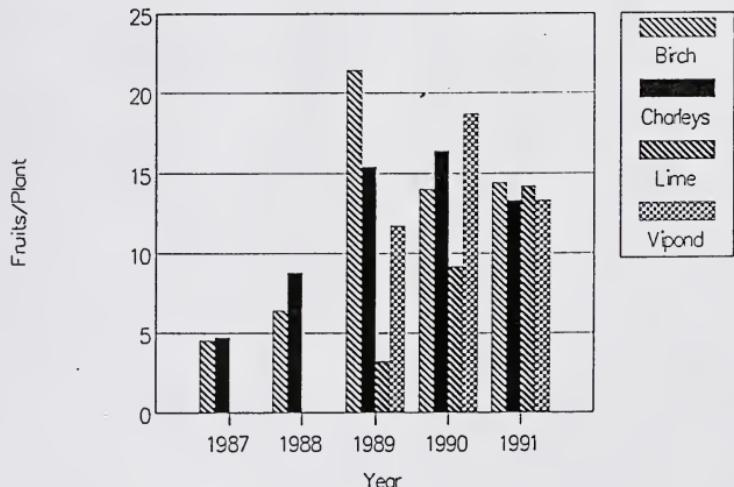
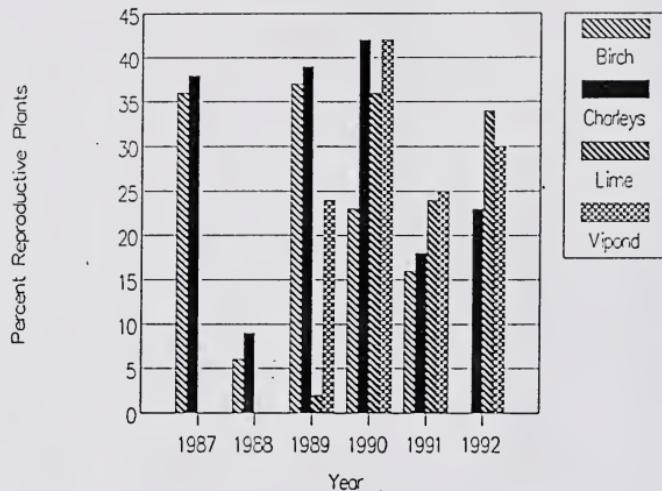


Figure 7. Fecundity (fruits/reproductive plant) of Arabis fecunda populations at four study sites in 1987-1992.



significant source of variation in fecundity (ANOVA; $N=1461$, $F=25.7$, $P<0.001$). None of the sites were significantly different from any others as determined by contrast test after the ANOVA ($P>0.15$), but Birch Creek and Vipond Park together, the two sites with the greatest overall fecundity, were significantly higher than Charleys Gulch and Lime Gulch ($P<0.001$).

The number of seeds per fruit varied from 5 to 56, and means varied from 26 ($SE=2.0$) at Vipond Park in 1990 to 38 ($SE=1.1$) at Birch Creek in 1987 (Table 2). The number of seeds per fruit differed significantly among years (ANOVA; $N=325$, $F=9.3$, $P<0.001$) but did not differ significantly among sites ($F=1.4$, $P=0.25$).

Weather and life history

Mortality was negatively associated ($N=15$, $r=-0.61$) and recruitment was positively associated ($N=15$, $r=0.48$) with winter precipitation. Higher fecundity (fruits/plant) was associated with warmer fall and winter temperatures and higher fall precipitation (multiple regression $r=0.78$, $N=19$).

Overall, there were few consistent relationships between weather and *Arabis fecunda* demographic parameters. The behavior of populations at different sites was highly idiosyncratic. For instance, mortality was well below normal at Birch Creek, Lime Gulch and Vipond Park in 1989-90 but was above average at Charleys Gulch. Recruitment was higher than average at Charleys Gulch and Lime Gulch in 1990-91 but was below normal at Birch Creek and Vipond Park. Fecundity was high at Birch Creek and Charleys Gulch in 1989 but was below average at Lime Gulch and Vipond Park.

DISCUSSION

Arabis fecunda appears to have two distinctive life-history strategies. Populations at Charleys Gulch and Lime Gulch showed similar demographic responses and had higher survivorship, lower mortality, lower recruitment rates and lower fecundity compared to populations at Birch Creek or Vipond Park. *Arabis fecunda* populations at Charleys Gulch and Lime Gulch had similar demography and were less variable in size and growth rate as well as demonstrating less variation in recruitment and mortality rates than those at Birch Creek or Vipond Park. Populations at Birch Creek and Vipond Park have a high variation strategy, while those at Charleys Gulch and Lime Gulch have a more stable state strategy.

Intraspecific differences in demography can be the result of genetic differentiation among populations and/or phenotypic plasticity. The existence of intraspecific ecotypes that differ

Table 2. Number of seeds per fruit (\pm SE) for Arabis fecunda at the four study sites in 1989-91.

	1989	1990	1991
Birch Creek	38.6 (1.1)	30.4 (1.1)	32.1 (1.1)
Charleys Gulch	32.3 (0.7)	31.2 (1.0)	31.8 (0.9)
Lime Gulch	31.1 (1.1)	34.3 (1.5)	33.8 (1.5)
Vipond Park	35.4 (1.6)	26.0 (2.1)	35.7 (2.0)

in demography has long been recognized (Turesson 1922, Clausen et al. 1940, Stebbins 1950), and different ecotypes can occur within short distances of each other (Solbrig and Simpson 1977). Under selection pressure from the environment, different populations can evolve divergent genotypes highly adapted to their surroundings. On the other hand an "all-purpose genotype" adapts to different environments by plastic responses in morphology, phenology and demography (Bradshaw 1965, Schlichting 1986). These two means of coping with environmental variability are not mutually exclusive, and either or both could be the source of variable demographic strategies in Arabis fecunda.

Regardless of the underlying mechanism causing demographic differentiation in Arabis fecunda, it is interesting to speculate on the environmental factors that drive the differentiation. The Birch Creek and Charleys Gulch populations occur at 1430-1530 m in elevation and are less than 10 km apart in the Sapphire Range. They are found in similar soils derived from the same geologic formation. Lime Gulch and Vipond Park are at 1890 and 2195 respectively and are ca. 30 km apart in the Pioneer Range. The two sites in the Pioneer Range are 130 km south of the two Sapphire Range sites. If abiotic factors such as weather or soils were determining life history strategies, we would expect there to be more similarity between the more geographically proximal sites, but this is not the case. The fact that the Birch Creek population is demographically more similar to Vipond Park than Charleys Gulch and that Charleys Gulch is more similar to Lime Gulch than Birch Creek indicates that abiotic factors, meteorological or edaphic, are not responsible for the demographic differentiation. Arabis fecunda habitats at Birch Creek and Vipond park have, on average, 15% more bare soil than those at Charleys Gulch and Lime Gulch, while the total cover of vascular plants is similar. Thus, A. fecunda populations that experience greater interspecific crowding are also the ones with higher and more variable demographic parameters.

Crowding has been shown to increase mortality of younger or smaller plants (Harper 1977, Powell 1990). Competition for water or nutrients could increase variability in mortality rate by amplifying the effects of adverse weather conditions. For example, a crowded population would be expected to suffer heavy mortality in a dry year, while a population that is not competing for water may not show such a large decrease in survivorship. In wet years, mortality at the two sites would be more similar. Recruitment of A. fecunda is enhanced by reduced interspecific competition (Lesica and Shelly 1992b) and should be lower in less crowded habitats. However, if differences between the two demographic strategies are under genetic control, increased fecundity and recruitment may have evolved to compensate for increased mortality in crowded habitats. Experimental work is needed to determine the basis for the two demographic strategies found in A. fecunda populations. Nonetheless, our results suggest

that there may be genetic differentiation for demographic parameters among populations of A. fecunda.

In many instances populations of Arabis fecunda at Birch Creek and Vipond Park had a different response than the other two populations to similar weather. In spite of this, our results suggest that winter precipitation is an important determinant of survivorship and recruitment. Low mortality often occurred in years with wet winters, and low recruitment often occurred following dry winters. The importance of winter precipitation could be in providing a protective blanket of snow during the coldest months or in providing ample early-season moisture. The importance of winter precipitation is probably at least partially responsible for the strong negative correlation between mortality and recruitment. There was no correlation between fecundity and recruitment or between fecundity and mortality ($N=15$, $r<0.08$). Higher fecundity was associated with above normal fall and winter temperatures and above normal fall precipitation. Since even in a poor year a reproductive plant produces an average of at least 120 seeds, it seems unlikely that year-to-year fluctuations in fecundity would have an important effect on population growth. Thus, it appears that winter precipitation is the most important weather variable affecting A. fecunda population growth.

MANAGEMENT IMPLICATIONS

A recent study of Arabis fecunda using isozyme markers suggests that there is little genetic differentiation among populations (Leeper et al. 1993). However, isozyme studies detect differentiation of neutral genotypes that occurs over relatively long periods of time. Genetic distance based on isozyme markers is generally related to length of time since population separation and degree of gene flow. Significant selection-driven differentiation can occur without differentiation among neutral alleles. Our study suggests the existence of ecotypic differentiation among A. fecunda populations. If differentiation does exist, a conservation strategy for this rare state endemic must strive to protect the genetic variation present among the many populations.

The Birch Creek and Vipond Park populations of Arabis fecunda demonstrated relatively large fluctuations in population size compared to those at Charleys Gulch and Lime Gulch. For example, population growth decreased in all populations in 1991; however, the decrease was less than 5% at Charleys Gulch and Lime Gulch but was 50-90% at Birch Creek and Vipond Park (Fig. 2). Populations subject to large fluctuations are generally thought to be more prone to extinction (Diamond 1984, Pimm et al. 1988). The Birch Creek and Vipond Park populations are large (Schassberger 19??), but smaller populations with the same demographic behavior may be at risk if prolonged stress occurs.

There is widespread agreement that increasing levels of atmospheric carbon dioxide and other "greenhouse gases" will result in global warming and widespread alteration of rainfall patterns during the next 50 years (Peters 1988, Henderson-Sellers 1990). Drier conditions are expected to cause a decrease in recruitment and an increase in mortality in Arabis fecunda populations. Warmer winters may result in some increase in fecundity and may partially offset the effects of drier conditions on mortality and recruitment. Nonetheless, if winter precipitation in southwest Montana decreases, populations of A. fecunda may decline. The greenhouse effect is also predicted to cause an increase in the variation of weather events (Schneider et al. 1992). Increased environmental variation could interact with the high demographic variation of some A. fecunda populations to increase the chances of extinction.

In summary, many populations of Arabis fecunda from a variety of habitats should be given protection to ensure maintenance of genetic diversity. Small populations that demonstrate widely fluctuating demographic behavior are less appropriate for long-term conservation purposes. Populations in relatively mesic habitats are expected to have longer persistence and should be given priority over those in drier sites.

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